

# WOOD AND BARK ANATOMY OF ACHATOCARPACEAE

Sherwin Carlquist

*Santa Barbara Botanic Garden  
1212 Mission Canyon Road  
Santa Barbara, CA 93105, U.S.A.*

## ABSTRACT

Qualitative and quantitative data are given for *Achatocarpus nigricans* Triana, *A. praecox* Griseb., and *Phaulothamnus spinescens* A. Gray. The minute vessel pits, lack of successive cambia, and lack of betalains or anthocyanins are distinctive features of the family that justify its removal from Phytolaccaceae. The phyletic nature of these features is unclear; libriform fibers are commonly regarded as specialized. The absence of borders on perforation plates accords with the placement of this family in suborder Phytolaccineae, however. Quantitative features of vessels accord with the concept that *Phaulothamnus* has the wood of a desert shrub, whereas wood of *Achatocarpus* is like that of a shrub from a chaparral-like habitat.

KEY WORDS: Achatocarpaceae, cambial phylogeny, Caryophyllales, ecological wood anatomy, Phytolaccaceae, systematic wood anatomy.

## RESUMEN

Se ofrecen datos cualitativos y cuantitativos sobre los leños de *Achatocarpus nigricans* Triana, *A. praecox* Griseb., y *Phaulothamnus spinescens* A. Gray. Punteaduras diminutas de vasos, deficiencia de pigmentos, y deficiencia de cambios sucesivos caracterizan a la familia, y separan Achatocarpaceae de Phytolaccaceae. El estado filético de estas peculiaridades es incierto; las fibras libriformes se interpretan como estado avanzado. Los datos cuantitativos de los vasos indican una ecología desertícola para *Phaulothamnus*, y una ecología de tipo chaparral seco para *Achatocarpus*.

## INTRODUCTION

Earlier systems include Achatocarpaceae (e.g., Walter 1909) within Phytolaccaceae sensu lato. The family was segregated by Heimerl (1934) so as to include one species of *Phaulothamnus* and nine of *Achatocarpus*, and has been thus recognized by most subsequent authors (Cronquist & Thorne 1994). The ovary of Achatocarpaceae has two stigmas but is unilocular and matures into a berry. This combination of features does not occur in Phytolaccaceae s.l. if Achatocarpaceae are segregated. More significantly, Achatocarpaceae are not known to produce either betalains or anthocyanins (Clement et al. 1994), whereas all other Phytolaccaceae s.l. contain betalains. All authors place Achatocarpaceae within Caryophyllales, but the position within the order is less clear. Placement of Achatocarpaceae just outside of suborder Phytolaccineae is currently commonly accepted (Manhart & Rettig 1994; Thorne in Cronquist & Thorne 1994; Behnke 1997), whereas Brown and Varadarajan (1985) place Achatocarpaceae outside Phytolaccaceae sensu stricto but inside Phytolaccaceae s.l.

The moderate degree of uncertainty in placement of Achatocarpaceae renders any



kind of data, including those from wood and bark anatomy, valuable for resolution of the phylogenetic relationships of the family. Data on wood and bark of Achatocarpaceae have been contributed by Metcalfe and Chalk (1950) and Gibson (1994). Molecular data are likely to provide strong evidence also; Caryophyllales are, as yet, relatively sparsely sampled with respect to DNA features.

The stem of species of Achatocarpaceae has a single cambium whereas several genera of Phytolaccaceae have successive cambia. Only a single cambium is known in the phytolaccaceous genera *Lophiocarpus*, *Microtea*, *Monococcus*, and *Trichostigma* (these genera would fall into Rivinaceae if Phytolaccaceae s. s. is reduced to *Anisomeria*, *Ercilla*, and *Phytolacca*). The question of whether successive cambia or a single cambium are plesiomorphic or apomorphic in Phytolaccaceae and in Caryophyllales as a whole remains to be resolved.

The concept of Caryophyllales offered by Cronquist and Thorne (1994) or Behnke and Mabry (1994) is used here. Plumbaginaceae and Polygonaceae are considered outgroups when the order is so designated (Rodman 1994). However, the data of Williams et al. (1994) have led a working group (APG 1998) to recognize an expanded Caryophyllales in which Plumbaginaceae, Polygonaceae, Tamaricaceae, Droseraceae, Nepenthaceae and allied families are included. The Cronquist and Thorne (1994) concept of Caryophyllales is then termed "core Caryophyllales." Wood and stem anatomy of Caryophyllales, when all families have been surveyed, may reflect the new classification or may tend to show subgroup patterns.

The present paper is part of a survey of wood anatomy of Caryophyllales that has included Caryophyllaceae (Carlquist 1995), Portulacaceae and Hectorellaceae (Carlquist 1998a), and Basellaceae (Carlquist 1999a). Among the genera or familial segregates of Phytolaccaceae s.l. studied to date are *Petiveria* and *Rivina* (Carlquist 1998b), *Agdestis* (Carlquist 1999b), *Stegnosperma* (Carlquist 1999c), *Barbeuia* (Carlquist 1999d), and rivinoid and phytolaccoid Phytolaccaceae (Carlquist in press). All of the families of Caryophyllales in the broad sense (APG 1998) will ultimately be included.

The two genera of Achatocarpaceae considered here are shrubs to small trees (Heimerl 1934). They are native to areas with dry seasons, most markedly so in the habitats of *Phaulothamnus* in southern Texas and northern Mexico, less extreme in the habitats of *Achatocarpus*, which range from Mexico to Argentina (Walter 1909; Heimerl 1934). The relationship of wood anatomy to the ecology of this family is a focus of the present paper.

#### MATERIALS AND METHODS

The collections studied are as follows: *Achatocarpus nigricans*, Portoviejo, Manabi, Ecuador (M. Acosta-Solis 11918), USw-0020137 (sample 22 mm in diameter); *A. praecox*, Tucumán, Argentina (sample 16 mm in diameter); *Phaulothamnus spinescens*, Sonora, Mexico, Jones 22596, POM (sample 5 mm in diameter). After softening with 4% aqueous ethylene diamine, sections were prepared with a sliding microtome and stained with a safranin-fast



green combination. Attempts to locate crystals were made with the use of polarizing equipment. Vessel diameter is measured as mean lumen diameter. Means for quantitative features reported are derived from 25 measurements per feature. Terminology for wood features accords with the IAWA Committee on Nomenclature (1964). Vessels per group is a mean based on a solitary vessel = 1, a pair of vessels in contact = 2, etc.

## RESULTS

### Wood Anatomy

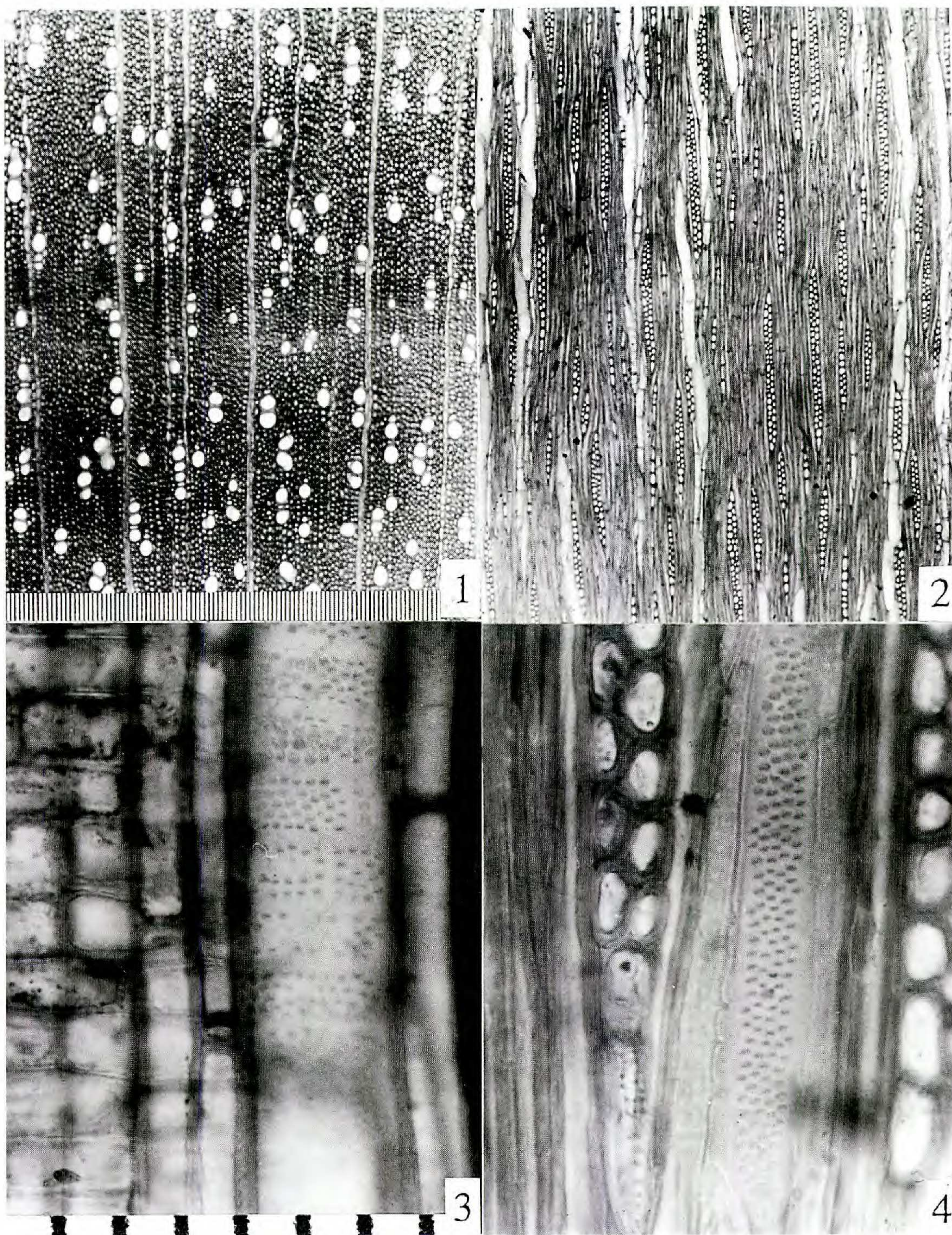
Both qualitative and quantitative features are given for *A. praecox*. Quantitative features are given for the two remaining species, but qualitative features are given for them only when these differ from the conditions in *A. praecox*.

*Achatocarpus praecox* (Figs. 1–4). Growth rings present but indistinct (Fig. 1). Vessels grouped in radial multiples or solitary; mean number of vessels per group, 1.78. Mean vessel lumen diameter, 30  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 88. Mean vessel element length, 292  $\mu\text{m}$ . Mean vessel wall thickness, 4.0  $\mu\text{m}$ . Perforation plates nonbordered. Perforation plates simple. Lateral wall pitting opposite on ray-vessel interfaces (Fig. 3), alternate on other vessel faces (Fig. 4). Lateral wall pits of vessels minute, about 1.5  $\mu\text{m}$  in diameter, circular in outline or nearly so, with small elliptical pit apertures. Imperforate tracheary elements are all libriform fibers with very small simple pits (Fig. 4, extreme left). Length of libriform fibers, 677  $\mu\text{m}$ . Mean wall thickness of libriform fibers, 2.5  $\mu\text{m}$ . Axial parenchyma vasicentric scanty, in strands of four cells (Fig. 3, to left and right of vessel). Rays both multiseriate and uniseriate (Fig. 2), the former more abundant. Mean height of multiseriate rays, 365  $\mu\text{m}$ . Mean width of multiseriate rays, 2.63 cells. Mean height of uniseriate rays, 119  $\mu\text{m}$ . Multiseriate rays composed of procumbent cells (Fig. 3, left; Fig. 4) except for tip cells (Fig. 4, lower left), which are square or upright. Uniseriate rays composed of procumbent or upright cells. Ray cell walls lignified, with mostly simple pits. Ray cell walls about 2.2  $\mu\text{m}$  thick. Wood nonstoried. Crystals absent. Starch not observed.

*Achatocarpus nigricans*. Mean number of vessels per group, 1.85. Mean vessel diameter, 37  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 17. Mean vessel element length, 273  $\mu\text{m}$ . Mean vessel wall thickness, 2.2  $\mu\text{m}$ . Mean vessel pit diameter, 1.7  $\mu\text{m}$ . Mean libriform fiber length, 670  $\mu\text{m}$ . Mean libriform fiber wall thickness, 1.5  $\mu\text{m}$ . Mean multiseriate ray height, 330  $\mu\text{m}$ . Mean width of multiseriate rays, 3.2 cells. Ray cell wall thickness about 1.1  $\mu\text{m}$ . Many vessels filled with amorphous yellow deposits. Libriform fibers commonly filled with amorphous yellow or dark deposits.

*Phaulothamnus spinescens* (Figs. 5–7). Vessels predominantly in radial groups or solitary (Fig. 5). Mean number of vessels per group, 2.78. Mean vessel diameter, 21  $\mu\text{m}$ . Mean number of vessels per  $\text{mm}^2$ , 347. Mean vessel element length, 354  $\mu\text{m}$ . Mean vessel wall thickness, 2.1  $\mu\text{m}$ . Mean vessel pit diameter, 1.8  $\mu\text{m}$ . Mean libriform fiber length, 549  $\mu\text{m}$ . Mean libriform fiber wall thickness, 1.1  $\mu\text{m}$ . Axial parenchyma is in strands of two cells. Uniseriate rays more common than multiseriate rays (Fig. 6). Mean height of multiseriate rays, 302  $\mu\text{m}$ . Mean width of multiseriate rays, 2.0  $\mu\text{m}$ . Mean height of uniseriate rays, 229





FIGS. 1–4. *Achatocarpus praecox*, wood sections. Fig. 1. Transection; vessels in center are slightly narrower, indicating inconspicuous growth ring. Fig. 2. Tangential section; rays are biseriata or uniseriate. Fig. 3. Radial section; an axial parenchyma strand touches the left side and another the right side of the vessel. Fig. 4. Tangential section; tip of biseriata ray, left; alternate minute pits on vessel. Figs. 1–2, scale below Fig. 1 (divisions = 10 μm); Figs. 3–4, scale below Fig. 3 (divisions = 10 μm).



$\mu\text{m}$ . Upright ray cells common, but procumbent ray cells also present (Fig. 7). Bordered pits common on tangentially oriented ray cell walls (Fig. 7). Ray cell wall thickness about  $1.1 \mu\text{m}$ . Amorphous deposits present in ray cells and in libriform fibers (Fig. 7).

### Bark

The sections of *Phaulothamnus spinescens* (Fig. 8) were unusually good and showed all regions of the bark clearly. The phellem cells (Fig. 8, top) contain dark-staining amorphous deposits. Several layers of phelloderm are present; cells of these layers are all thick walled sclereids (Fig. 8). Outer cortex composed of tangentially widened parenchyma cells with nonlignified cell walls. Inner cortex composed of a continuous cylinder of thick-walled sclereids. Scattered fibers present in older secondary phloem (Fig. 8).

The bark of *A. praecox* is similar to that of *P. spinescens*. In *A. praecox*, however, both an outer and an inner cylinder of thick walled cortical sclereids are present. The more complex bark of *A. praecox* may be related to large diameter of the sample studied here.

### DISCUSSION AND CONCLUSIONS

Of all families once included in Phytolaccaceae, the family most universally segregated is Achatocarpaceae. In fact, the molecular results of Manhart and Rettig (1994) and the cladistic and phenetic studies of Rodman (1994) showed that Achatocarpaceae are not, in most analyses, a sister group of Phytolaccaceae, and might even be in a near-basal position in Caryophyllales (as defined by Behnke & Mabry 1994). Achatocarpaceae are not known to contain either betalains or anthocyanins (Clement et al. 1994); this is also true of *Barbeuia*. In two caryophyllalean families, Caryophyllaceae and Molluginaceae, anthocyanins are present but betalains are absent.

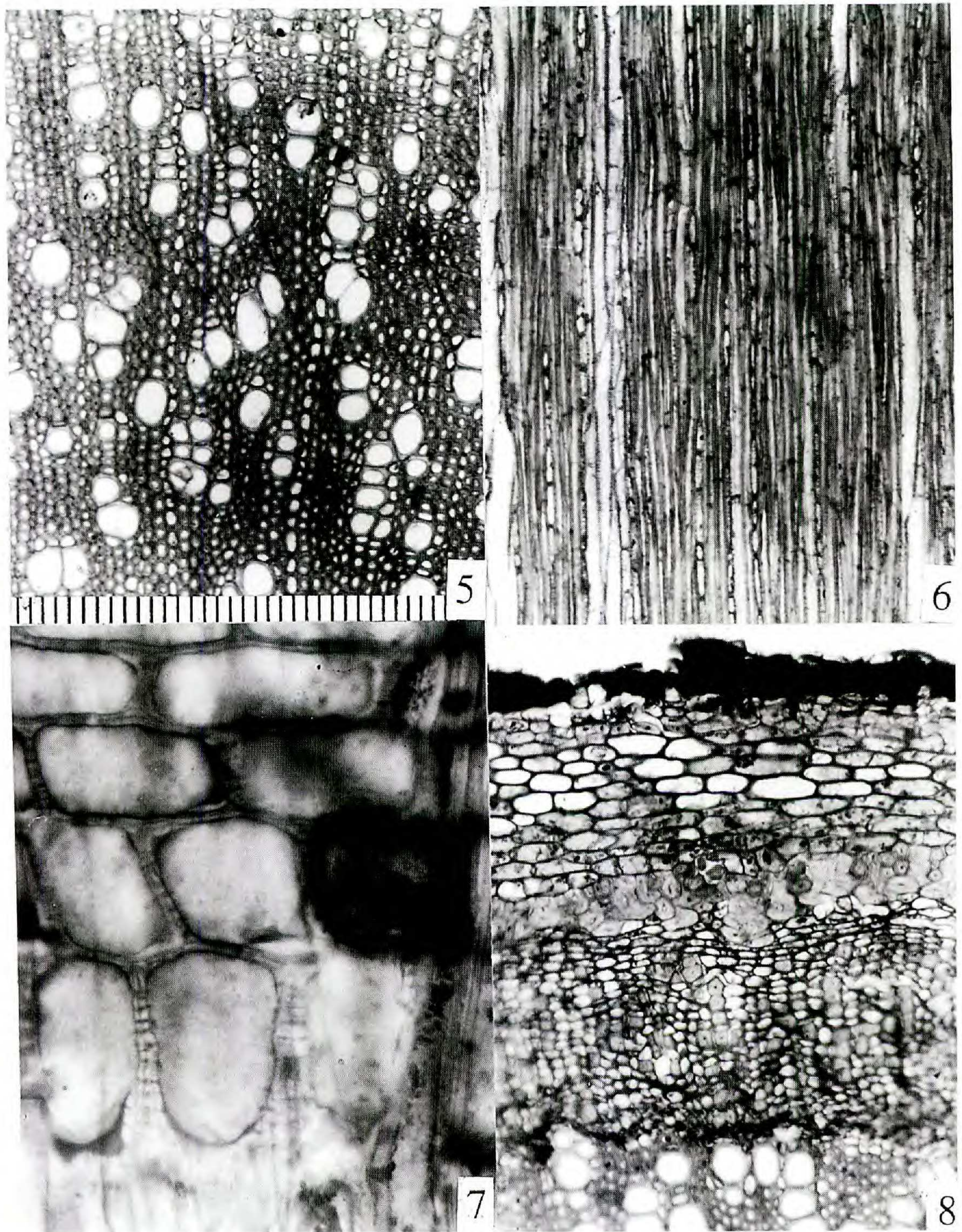
The data from wood anatomy suggest that Achatocarpaceae belong to Caryophyllales: absence of borders on perforation plates characterizes Achatocarpaceae and also most families of Caryophyllales investigated thus far (Carlquist 1998b, 1999b, 1999c, in press). Bark data are not available yet for a large enough number of caryophyllalean genera so that they can be presented as evidence for the familial composition of Caryophyllales or the position of Achatocarpaceae within the Caryophyllales.

The libriform fibers of Achatocarpaceae are a specialized feature in dicotyledons according to traditional criteria (Metcalfe & Chalk 1950, p. xlv), whereas tracheids, shown by Metcalfe and Chalk (l.c.) to be more primitive, occur in families often claimed to occupy near-basal positions in the order: Caryophyllaceae (Carlquist 1995), Stegnospermataceae (Carlquist 1999c), and Barbeuiaceae (Carlquist 1999d). All of these families, however, have successive cambia (Caryophyllaceae only in some genera), whereas Achatocarpaceae does not. Whether absence of betalains and absence of successive cambia are plesiomorphic or apomorphic is uncertain.

The presence of very small pits on vessels of Achatocarpaceae is a feature not reported elsewhere in Caryophyllales (Metcalfe & Chalk 1950; Gibson 1994). The minute pits are indicative of the distinctiveness of Achatocarpaceae as a family.

The rays of *Achatocarpus* can be characterized as Heterogeneous Type IIB, transi-





FIGS. 5–8. *Phaulothamnus spinescens*, sections of wood (5–7) and bark (8). Fig. 5. Transection; vessels are mostly grouped. Fig. 6. Tangential section; rays inconspicuous, composed mostly of upright cells. Fig. 7. Radial section, procumbent ray cells at top, upright cells at bottom. Fig. 8. Transection, phellem at top, secondary xylem at bottom; outer cortex consists of oval parenchyma cells, inner cortex is comprised of pale gray fibers. Figs. 5, 6, 8, scale below Fig. 5 (divisions = 10  $\mu$ m); Fig. 7, scale below Fig. 3.



tional to Homogeneous Type I (Kribs 1935; Carlquist 1988). The predominance of upright ray cells in the *Phaulothamnus* specimen studied is related to the small diameter of that specimen and is indicative of a juvenile condition (see Carlquist 1988) and not phylogenetically different from the conditions shown by the comparatively larger *Achatocarpus* specimens, which exhibit a rather more mature pattern.

The moderate to high degree of vessel grouping in the three species is indicative of moderate to marked xeromorphy (Carlquist 1984). This is independently evident in the Mesomorphy Ratio (vessel diameter times vessel element length divided by number of vessels per mm<sup>2</sup>), a convenient expression of both conductive safety and conductive efficiency. The values for this ratio are: *A. nigricans*, 59; *A. praecox*, 99; *P. spinescens*, 21. The desert or near-desert habitats of *Phaulothamnus* correlate with the low values for that species. Southern California desert shrubs as a group have a Mesomorphy Ratio of 20.9 (Carlquist & Hoekman 1985). The higher values for *Achatocarpus* are close to the values for southern Californian chaparral shrubs as a group, 66.7, or southern Californian coastal sage shrubs, 80.7 (Carlquist & Hoekman 1985).

#### REFERENCES

- APG (ANGIOSPERM PHYLOGENY GROUP). 1998. An ordinal classification for the families of flowering plants. *Ann. Missouri Bot. Gard.* 85:531–553.
- BEHNKE, H.-D. 1997. Sarcobataceae—a new family of Caryophyllales. *Taxon* 46:495–507.
- \_\_\_\_\_ and T.J. MABRY (eds). 1994. *Caryophyllales. Evolution and systematics*. Springer Verlag, Berlin & Heidelberg.
- BROWN, G.K., and F.S. VARADARAJAN. 1985. Studies in Caryophyllales 1: Re-evaluation of classification of Phytolaccaceae s.l. *Syst. Bot.* 10:49–63.
- CARLQUIST, S. 1984. Vessel grouping in dicotyledon woods: Significance and relationship to imperforate tracheary elements. *Aliso* 10:505–525.
- \_\_\_\_\_. 1988. *Comparative wood anatomy*. Springer Verlag, Berlin & Heidelberg.
- \_\_\_\_\_. 1995. Wood anatomy of Caryophyllaceae: Ecological, habitat, systematic, and phylogenetic implications. *Aliso* 14:1–17.
- \_\_\_\_\_. 1998a. Wood anatomy of Portulacaceae and Hectorellaceae: Ecological, habitat, and systematic implications. *Aliso* 16:137–153.
- \_\_\_\_\_. 1998b. Wood and stem anatomy of *Petiveria* and *Rivina* (Caryophyllales): Systematic implications. *IAWA J.* 19:383–391.
- \_\_\_\_\_. 1999a. Wood, stem, and root anatomy of Basellaceae, with relation to systematics and cambial variants. *Flora* 194:1–12.
- \_\_\_\_\_. 1999b. Wood anatomy of *Agdestis* (Caryophyllales): Systematic position and nature of the successive cambia. *Aliso* 18:35–43.
- \_\_\_\_\_. 1999c. Wood and stem anatomy of *Stegnosperma* (Caryophyllales): Phylogenetic relationships; nature of lateral meristems and successive cambial activity. *IAWA J.* 20:149–163.



- \_\_\_\_\_. 1999d. Wood anatomy, stem anatomy, and cambial activity of *Barbeuia* (Caryophyllales). IAWA J. 20:431–440.
- \_\_\_\_\_. (In press). Wood and stem anatomy of phytolaccoid and rivinoid Phytolaccaceae (Caryophyllales): ecology, systematics, nature of successive cambia. Aliso \_\_\_\_\_, and D.A. Hoekman. 1985. Ecological wood anatomy of the woody southern California flora. IAWA Bull., n.s., 6:319–347.
- CLEMENT, J.S., T.J. MABRY, H. WYLER, and A.S. DREIDING. 1994. In: H.-D. Behnke and T.J. Mabry, eds. Caryophyllales. Evolution and systematics. Springer Verlag, Berlin & Heidelberg. Pp. 247–261.
- CRONQUIST, A. and R.F. THORNE. 1994. Nomenclatural and taxonomic history. In: H.-D. Behnke and T.J. Mabry, eds. Caryophyllales. Evolution and systematics. Springer Verlag, Berlin & Heidelberg. Pp. 5–25.
- GIBSON, A.C. 1994. Vascular tissues. In: H.-D. Behnke and T.J. Mabry, eds. Caryophyllales. Evolution and systematics. Springer Verlag, Berlin & Heidelberg. Pp. 45–74.
- HEIMERL, A. 1934. Achatocarpaceae. In: A. Engler & H. Harms, Die natürlichen Pflanzenfamilien, ed. 2, 16c:174–178. Verlag von Wilhelm Engelmann, Leipzig.
- IAWA COMMITTEE ON NOMENCLATURE. 1964. Multilingual glossary of terms used in wood anatomy. Verlagsbuchanstalt Konkordia, Winterthur, Switzerland.
- KRIBS, D.A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. 96:547–557.
- MANHART, J.R., and J. H. RETTIG. 1994. Gene sequence data. In: H.-D. Behnke and T.J. Mabry, eds. Caryophyllales. Evolution and systematics. Springer Verlag, Berlin & Heidelberg. Pp. 235–246.
- METCALFE, C.R. and L. CHALK. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford.
- RODMAN, J. E. 1994. Cladistic and phenetic studies. In: H.-D. Behnke and T.J. Mabry, eds. Caryophyllales. Evolution and systematics. Springer Verlag, Berlin & Heidelberg. Pp. 279–301.
- WALTER, H. 1909. Phytolaccaceae. Das Pflanzenreich IV(83):1–154.
- WILLIAMS, S.E., V.A. ALBERT, and M.W. CHASE. 1994. Relationships of Droseraceae: A cladistic analysis of *rbcl* sequence and morphological data. Amer. J. Bot. 81:1027–1037.